SENSORY ORGANS IN THE HAIRY GIRDLES OF SOME MOPALIID CHITONS

By: Esther M. Leise

Leise, E.M. (1988) Sensory organs in the hairy girdles of some mopaliid chitons. *American Malacological Bulletin* 6(1):141-151.

Abstract:

The polyplacophoran mantle secretes the shell plates, houses the gills in the pallial grooves, and forms a muscular perinotum or girdle that encircles the shell and viscera. The epidermis of this girdle occurs as papillae of columnar cells dispersed over an otherwise cuboidal epithelium. Depending upon the species, these papillae can produce a variety of hard structures: calcareous scales, spicules, or spines and/or chitinous hairs. Some papillae also produce bulbous outgrowths called nodules or "morgensternförmigen Körper" (morning star-shaped bodies). These nodules contain the dendrites of sensory neurons and are thought to be mechanoreceptive. Nodules can occur alone in the cuticle or in conjunction with calcareous spicules. Nodules of this type are present in the hairs of chitons in the genus *Mopalia*. Hairs from other mopaliid genera are also innervated, although they can lack these particular structures. In most species of chitons that I examined, nodules are made in conjunction with the ventral girdle spicules and the marginal spicules. These presumptive mechanoreceptors could be ubiquitous among chitons, as all species possess marginal spicules and overlapping ventral spicules. Hairs could have evolved to extend the reach of these tactile receptors beyond the surface of the animal's body, as well as to provide mechanical protection from desiccation and predation.

Article:

The external surfaces of the polyplacophoran girdle are armed with diverse types of secreted structures whose form and arrangement is species specific. These secretions include calcareous spicules, spines, and scales, and chitinous hairs (Fischer-Piette and Franc, 1960) (Figs. 1, 2). The dorsal surface can produce several types of hard parts, while the mantle edge and ventral surfaces generally produce one type of ornament each (Hyman, 1967). These structures can be completely or partially embedded in the cuticle that covers the epidermal cells of the girdle. These girdle formations, or ornaments, can be simple or composite structures (Fig. 1). Individual, fusiform, calcareous spicules are often totally embedded in the cuticle, which is 25 to 100μm thick, whereas longer calcareous spines (Figs. 1, 2b) have only their proximal ends in the cuticular matrix (Plate, 1898, 1902; Hyman, 1967). Many species produce overlapping calcareous scales (Fig. 2a) that are also connected to the cuticle basally. Species in several families produce hairs (Fig. 2c), often called setae or bristles, that can be simple, jointed (articulated), or composite chitinous shafts that extend beyond the girdle surface. Hairs usually consist of an extension of the cuticular matrix and can be surrounded by a more densely staining cortex (Leise and Cloney, 1982).

Most spicules are surrounded by a layer or "cup" of material that is darker than the enveloping cuticular matrix and stains more densely in sectioned material (Figs. 1, 3) (Plate, 1898, 1902; Knorre, 1925; Leise and Cloney, 1982). In spicules from many species, this dense cup is elongated into a shaft that extends from the spicule to the epidermal cells (Fig. 1). The similarity of many hairs to this type of spicule shaft and the presence of a spicule at the distal tip of many hairs, led Thiele (1929) and Hyman (1967) to suggest that spicules and hairs represent the two ends of a continuum of girdle structures. They regard hairs as highly modified shafts of spicules. I continue their usage here and refer to hairs as those structures in which a chitinous shaft projects above the surface of the girdle and is the predominant part of the organ.

As will be described below, most hairs contain or are in contact with dendrites from presumptive sensory neurons. This paper reviews the morphology of chiton hairs while focusing on their neuronal elements and describes the relationships of these hairs to other girdle ornaments.

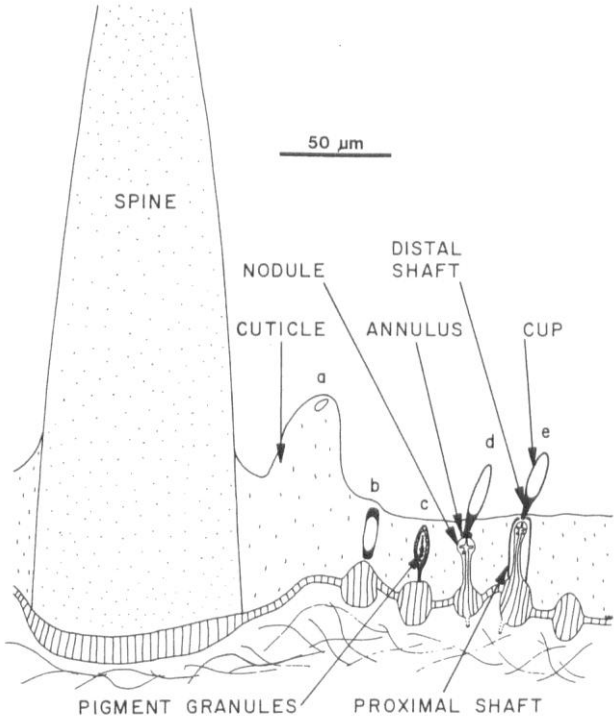


Fig. 1. Diagram of five types of spicules and one spine. **a.** Primary spicule from a newly metamorphosed juvenile. Note thin chitinous cup. **b.** Spicule with apically and basally thick cup. **c.** Spicule with pigment granules and shaft. **d.** Spicule with an annulate shaft surmounting a sensory nodule. **e.** Spicule as in d but with an articulated shaft (from Leise, 1983).

DIVERSE GIRDLE HAIRS: AN OVERVIEW

Hairs occur in a bewildering range of sizes and configurations in species from at least five families: Chitonidae; Lepidochitonidae (Ferreira, 1982); Callochitonidae; Chaetopleuridae; and Mopaliidae [classification after Bergenhayn (1955) unless otherwise cited]. In addition, hairs from many species of chitons will erode during the animal's lifetime. Thus' it can be difficult to understand the morphology of a particular type of hair if only large hairs or hairs from old animals are studied. Species such as *Chiton olivaceus* Spengler, 1797 (family Chitonidae) can produce small marginal hairs 80 to 100μm long (Plate, 1902). In the Lepidochitonidae (Ferreira, 1982) species such as *Tonicella insignis* Reeve, 1847 produce small, simple hairs only 100μm long (Leise, 1983), while others, such as *Dendrochiton lirulatus* Berry, 1963, produce tufts of hairs up to 500μm long. Hairs from species of Callochitonidae, such as *Eudoxochiton nobilis* Gray, 1843, often have large articulated shafts about 1.5 mm in length (Leise, 1983). On in. tact animals of *E. nobilis*, even the distal spicules can be discerned. Species in the Chaetopleuridae and Mopaliidae also display hairs in a wide range of sizes; although the Chaetopleuridae characteristically produce hairs (Pilsbry, 1893), some species, like *Chaetopleura lurida* (Sowerby, 1832) secrete none. The girdle of this species bears spicules with articulated and simple shafts. A congener, C. *peruviani* Lamarck, produces similar spicules whose elongated shafts extend beyond the cuticular surface and so earn them the designation of hair (Plate, 1902; Fischer-Piette and Franc, 1960) (Fig. 4). Among the Mopaliidae are also species that produce small, simple hairs, such as those on *Katharine tunicata* Wood, 1815 or very large, simple hairs, as are found on *Plaxiphora obtecta* (Carpenter in Pilsbry, 1893) (Table 1).

Most of the above mentioned hairs conform to the hypothesis of Thiele (1929) and Hyman (1967) that hairs are elongated spicule shafts. However, the large hairs secreted by species in the genera *Mopalia* and *Placiphorella*, and those secreted by some of the Lepidochitonidae, namely *Lepidochitona flectens* (Carpenter, 1864), and species in the genus *Dendrochiton* Berry, 1911 (Ferreira, 1982), do not conform to Thiele's (1929) and Hyman's (1967) hypothesis. These latter types of hairs are composite structures, built by the replication of many basic

units. They are not simply enlarged or elongated spicule shafts. In the genus *Mopalia*, the basic unit construct is a calcareous spicule and its long chitinous shaft This basic unit is serially repeated along an outgrowth of the cuticle, and with the exception of the groove along which these spicules lie, the entire organ is surrounded by one or two distinct layers of dense cortical material (Fig. 5) (Leloup, 1942; Leise and Cloney, 1982). Similarly, in the genus *Placiphorella*, the hair is an extension of the cuticle and is entirely covered with spicules that lie in whorls just below the surface of the hair (Fig. 2c) (Plate, 1902). From Ferreira's (1982) descriptions, the hairs of *L. flectens* and the genus *Dendrochiton* appear likewise to be branched or compound structures and not simply enlarged spicule shafts.

Table 1. Characteristics of chitons hairs in the family Mopaliidae (Structure: C = compound; S = simple and lacking medulla. Length and width are maxima recorded. Cortex: ++ = >20 μm thick; + = <20 μm thick; − = lacking).

Species	Hair Length (mm)	Hair Width (μm)	Structure	Cortex	Innervation
Mopalia muscosa	5	400	C	++	+
M. ciliata	3	200	C	++	+
M. lignosa	3	300	C	+	+
M. hindsii	2.5	80	C	+	+
Plaxiphora obtecta	2	300	S	++	−
Katharina tunicata	0.1	5	S	+	+
Placiphorella velata	5	400	C	−	+

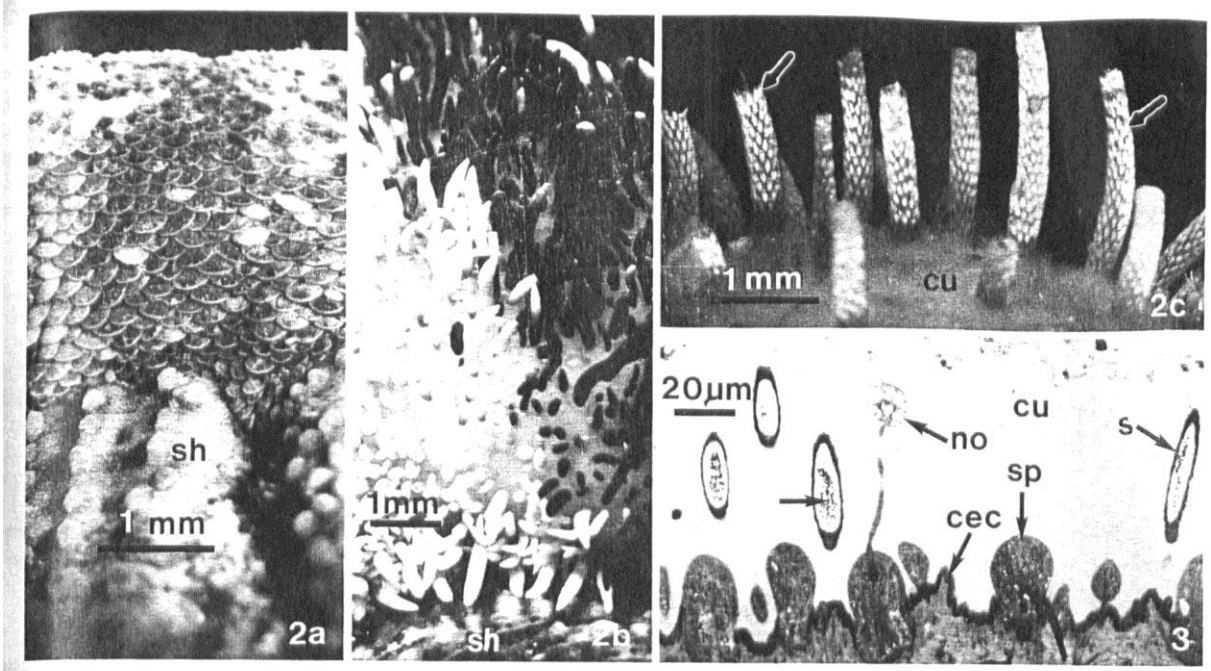


Fig. 2. a. Dorsal integument of *Lepidozona cooperi* (Pilsbry, 1892) demonstrating overlapping scales. **b.** Dorsal integument of *Acanthopleura granulata* (Gmelin, 1791) displaying calcareous spines. Cuticle is visible between spines. **c.** Dorsal hairs of *Placiphorella velata*. Numerous spicules (arrows) are embedded near the surface of each hair (cu, cuticle; sh, shell) (from Leise, 1983). **Fig. 3.** Transverse 1 μm section through the decalcified integument of *Mopalia muscosa*. Spicules (s) produced by spiniferous papillae (sp) contain brown pigment granules (arrow). One spiniferous papilla has produced a sensory nodule (no). Part of its stalk is not in the plane of this section. Common epidermal cells (cec) occur between papillae (from Leise and Cloney, 1982).

THE MORPHOLOGY OF HAIRS OF *MOPALIA MUSCOSA:* A MODEL FOR COMPOSITE SENSORY HAIRS

A fully-formed hair of *Mopelia muscosa* is a curved, distally tapered extension of the cuticle that bears a mesial groove in which lies a row of spicules (Figs. 5, 6). Each spicule occurs atop a distinct shaft, whose proximal end is embedded in the cuticular matrix, or medulla. The medulla as enveloped by a bilayered cortex, except for the mesial groove, and is therefore exposed to the environment along the length of that groove. Within the medulla, the proximal end of each spicule shaft surmounts a bulbous epidermal projection, a stalked nodule (Leise and Cloney, 1982) or morgensternförmig Körper" (morning star-shaped body) (Reincke, 1868). Blumrich (1891), Knorre (1925), and Plate ([18]98, 1902) described such nodules in many species. All of [t]hese authors suggest that the nodules are tactile. Until recently (Leise and Cloney, 1982), their presence in hairs of the Mopaliidae was unknown.

The dorsal girdle epidermis is a single layer of cells that is divided into numerous packets or papillae of columnar cells. These papillae produce the hairs, spicules, and nodules. Smaller cuboidal cells occur ubiquitously between the papillae. The papillae that produce the hairs are the largest in the epidermis and as a hair matures, the papilla comes to lie in a small depression or pocket below the level of the rest of the epidermal cells (Leise and Cloney, 1982; Leise, 1986).

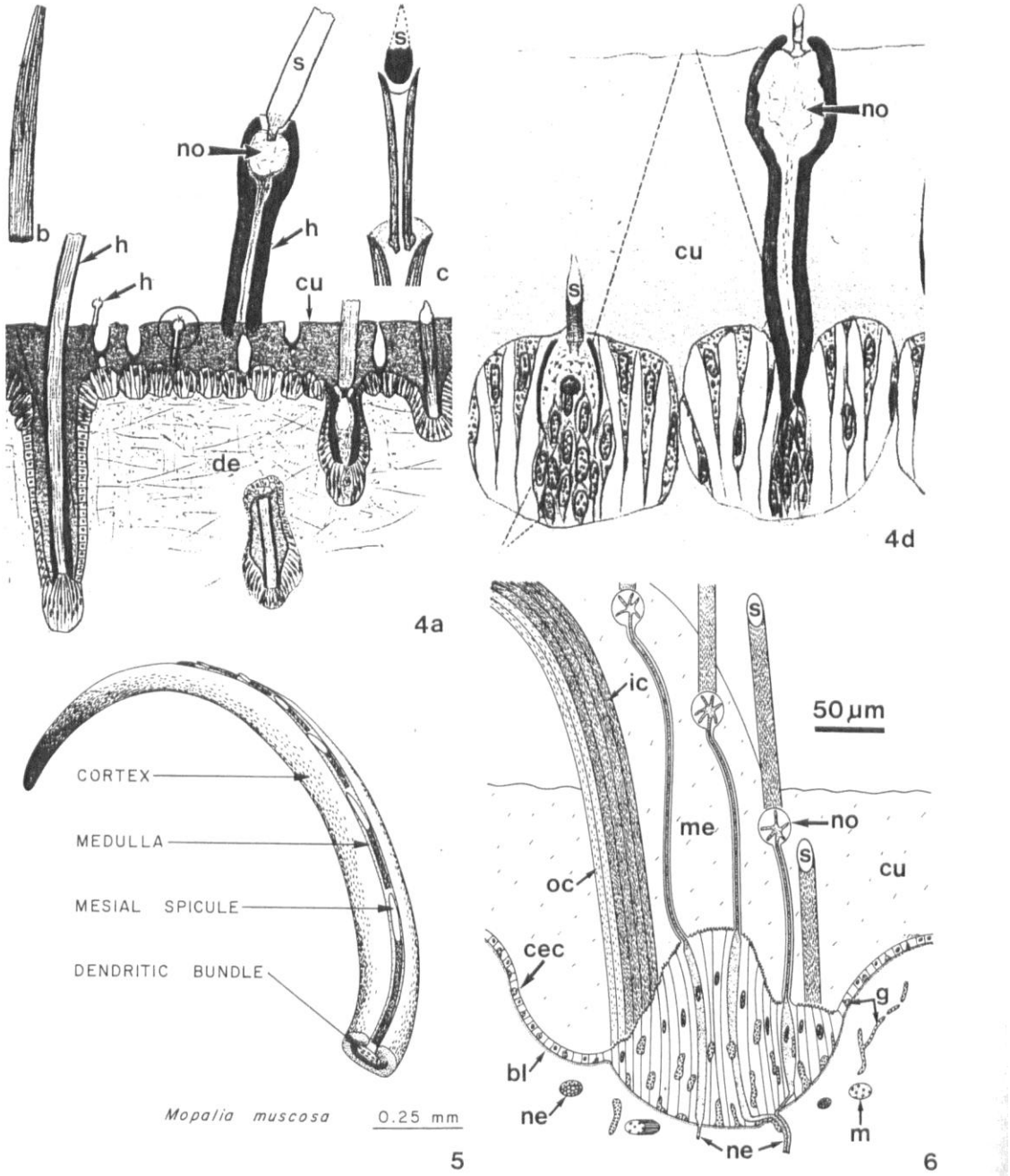


Fig. 4. a-d. Diagram of spicules and hairs of *Chaetopleura peruviana.* **a.** Three hairs (h) occur above the cuticle (cu). All three hairs are simple; the right two are each capped by a spicule (s) and appear to contain stalked nodules (no). **b.** Tip of a simple hair. **c.** Tip of an articulated hair with distal spicule (s). **d.** Enlargement of the small spicule circled in a whose shaft contains a stalked nodule (no) (de, dermis) (from Plate, 1902). **Fig. 5.** Diagram of the external morphology of a hair of *Mopalia muscosa.* The base of the shaft of each mesial spicule is embedded in the medulla. Below each shaft is an epidermal sensory nodule. The cut ends of the nodule stalks are visible in the medulla. The hair is drawn in its entirety as if it were cut off just beyond the cuticle (from Leise, 1986). **Fig. 6.** Diagrammatic longitudinal section through the base of a hair of *Mopalia muscosa*, drawn passing through the mesial groove and two spicules (s). Dendrites from three sensory neurons terminate in nodules (no). In mature hairs, the sensory neurons occur in clusters, not as single cells, as they are drawn here, for clarity. Two nerves (ne) cross the basal lamina (bl) as they emerge from the base of the papilla (cec, common epidermal cells; cu, cuticle; g, pigmented glial cells; ic, inner cortex; m, muscle fiber; me, medulla; oc, outer cortex).

Each subcortical cell produces a bundle of cortical fibers (Figs. 6, 7). The fiber bundles of the inner cortex are more dense than those of the outer cortex (Leise and Cloney, 1982). Each layer of the cortex in a mature hair is several bundles thick, whereas in young hairs the cortex is only one bundle wide. Newly forming hairs have no

cortex and start as a single spicule with an elongated shaft that lies above a stalked nodule. More spicules and their associated shafts and nodules are added to the growing cuticular hair and only after several nodules are present does cortex begin to appear. The cortex is initially a narrow crescent along the lateral edge of the hair. As development proceeds, the hair grows longer and the cortex become progressively wider until it encompasses nearly the entire shaft (Leise, 1986).

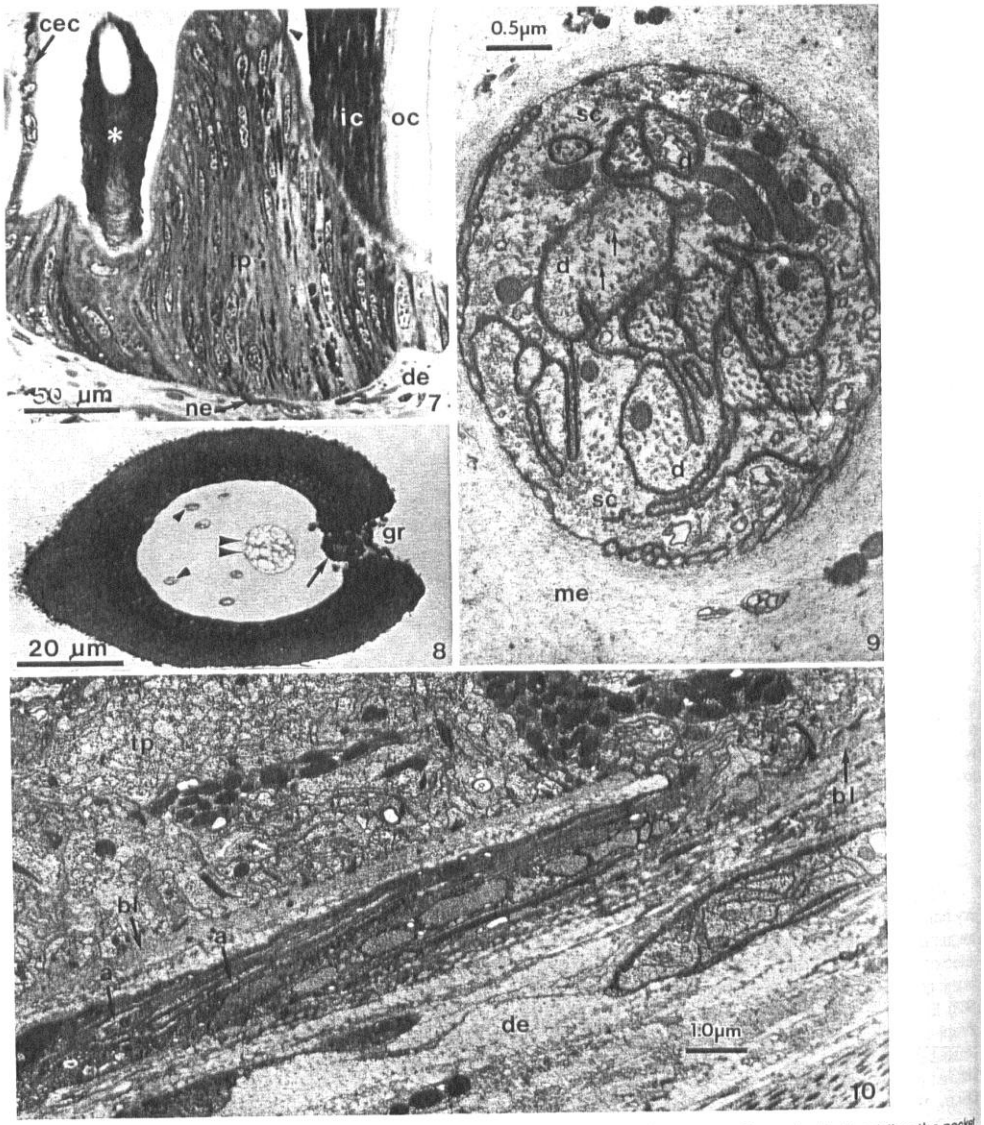


Fig. 7. Median longitudinal 1 µm section through the base of a girdle hair of *Mopalia muscosa*. Common epidermal cells (cec) line the pocket in which the trichogenous papilla (tp) lies. This section grazes the shaft (asterisk) of a mesial spicule (c.f. Fig. 6). The continuity of the medulla and cuticle is visible just above this shaft. The proximal end of the dendritic stalk of a sensory nodule is emerging from the papilla (arrowhead). One nerve (ne) emerges from the base of the papilla and enters the dermis (de) (ic, inner cortex; oc, outer cortex) (from Leise and Cloney, 1982). **Figs. 8.** Transverse 1 µm section through a hair of *Mopalia muscosa*, above the cuticle. Six dendritic bundles (arrowheads) and one nodule (double arrowheads) lie in the medulla. The groove (gr) in the cortex exposes the medullary matrix to the environment and is broader in younger hairs. The shaft (arrow) of the last mesial spicule lies just inside the groove (from Leise and Cloney, 1982). **Fig. 9.** Transverse section through the stalk of a sensory nodule from a hair of *Mopalia muscosa*. Numerous dendrites (d) are enclosed by two supporting cells (sc). The dendrites contain numerous parallel microtubules (arrows) and mitochondria (me, medulla). **Fig. 10.** Axons (a) emerge from the base of a trichogenous papilla (tp). The nerve passes into the dermis (de) from the base of the papilla. Note that the epidermal basal lamina (bl) does not surround the nerve.

Submedullary cells occur as a hillock that protrudes into the base of the hair shaft and presumably secrete the medullary matrix. The sensory cells lie in clusters within this hillock and each cluster produces a long bundle of dendrites oat extends through the hair (Figs. 6-9) (Leise and Cloney, 1982). The oldest dendritic bundle extends to the tip of the hair; younger bundles are progressively shorter. Each dendritic bundle ends in a nodule, just below the shaft of a mesial spicule (Fig. 6). A hair can have from one to 20 nodules in arising from the same number of neuronal clusters in the submedullary hillock (Leise and Cloney, 1982). One or several nerves emerge from the base of each trichogenous (hair-producing) papillae (Figs. 6, 7, 10). These nerves are preesumed to contain the axons of the submedullary sensory neurons (Fig. 10). Although these basal axons have not been definitively shown to arise from the neurons (i.e. the submedullary neurons could be axonless,

synapsing upon sensory interneurons from the CNS, or the submedullary 'neurons" could have been misidentified and the nerves could have other functions) (see also following section), the most obvious explanation is that the epidermal cells whose long apical necks contain numerous parallel microtubules are primary sensory neurons (Leise and Cloney, 1982). Finally, there are usually fewer nerves than nodules within one papilla, indicating that the axons from several clusters of neurons converge onto a single nerve (Fig. 6).

Each nodule (and hence each dendritic bundle) contains dendrites from several cells, there being from one to 25 dendrites per bundle (Fig. 9) (Leise and Cloney, 1982). Each bundle is surrounded by one or two submedullary supporting cells. The dendrites often branch, so a tally of the number 01 dendrites in a bundle overestimates the number of sensory neurons. In figure 6 the sensory dendrites are drawn as straight cylinders with only one neuron per cluster for ease of presentation. Within the nodule, the dendrites ramify between the processes of the submedullary supporting cells that contain large vacuoles (Fig. 11).

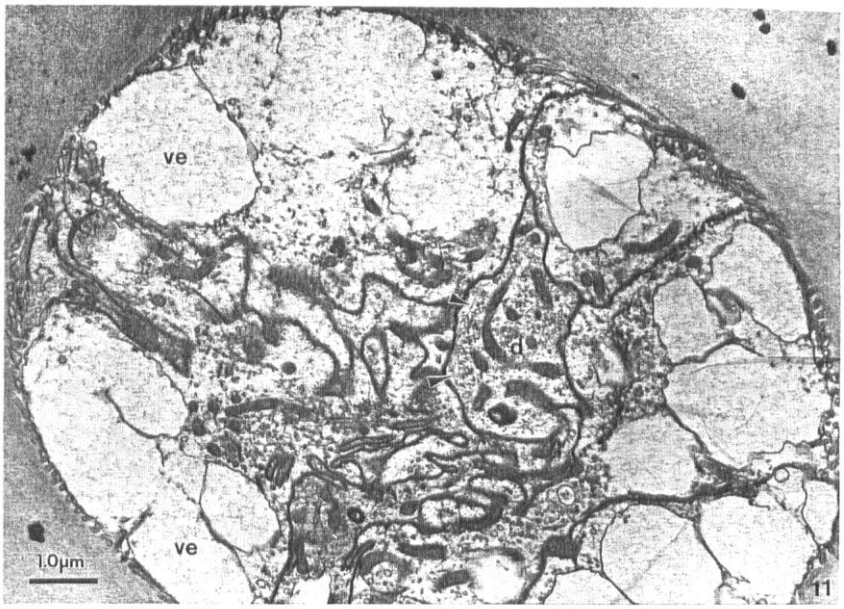


Fig. 11. Electron micrograph of a sensory nodule from a hair of *Mopalia muscosa.* In nodules, the dendrites (d) lose their typical organization; their mitochondria are twisted and the microtubules are no longer in parallel arrays (arrowheads). Large electron-lucent vacuoles (ve) lie around the periphery within the surrounding cells.

SENSORY HAIRS FROM OTHER MOPALIIDAE

To gain some understanding of the occurrence of sensory hairs throughout the Mopaliidae, I examined the girdle integuments of six other species in this family. Animals were collected from rocky intertidal regions in Puget Sound, Washington, or on Vancouver Island, British Columbia (Leise, 1983). Samples of girdle integuments were fixed in Millonig's phosphate buffered glutaraldehyde and post-fixed in bicarbonate buffered osmium tetroxide (Cloney and Florey, 1968). Detailed procedures are described elsewhere (see Leise and Cloney, 1982; Leise, 1983). Specimens of *Plaxiphora obtecta* were obtained indirectly from New Zealand, where they were fixed in 5% formalin in seawater.

In addition to various shell and body characteristics, one of the mopaliid diagnostic features is the production of dorsal girdle hairs. From most accounts, the one exception In this hairy family appeared to be *Katharina tunicata.* However, Leloup (1940) noticed that the girdle of this species produces tiny translucent hairs (Table 1). I confirmed this observation and found that the papillae that secrete these hairs are also innervated (Fig. 12).

Three other species of *Mopalia,* namely *M. ciliata, M. hindsii,* and *M. lignosa,* have innervated hairs similar to those of M. *muscosa* (Fig. 13). Interspecific variation occurs in size, number of nodules per hair, extent of cortical envelopment, and size and arrangement of spicule shafts (Leise, 1983).

The hairs of *Placiphorella velata* Dail 1878 (Fig. 2c) are quite different from those in the genus *Mopalia. Placiphorella* hairs contain no nodules, although they are innervated (Plate, 1902; Leise, 1983). Instead of lying

above a nodule, each spicule in these hairs lies above a cell that projects beyond the hillock on a thin stalk (Fig. 14). The ultrastructure of these cells deserves attention as they too are likely to be sensory neurons. *As* Plate (1902) reported for *P stimpsoni* (Gould, 1859), several nerves emerge from the epidermis below each of the hairs of *P velata.* Again, these nerves probably carry axons from the primary sensory neurons, and axons from many neurons converge into each nerve.

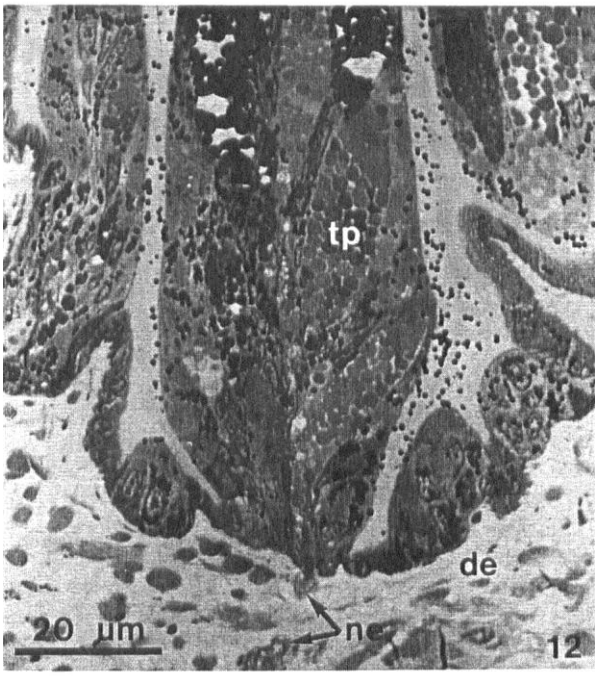


Fig. 12. Longitudinal 1 µm section through the base of a trichogenous papilla (tp) of *Katharina tunicata.* One nerve (ne) emerges from the base of the papilla then continues into the dermis (de) (from Leise, 1983). Many cells of these papillae also produce granules, which can be seen here in their various stages of condensation. Eventually, granules are extruded into the cuticle.

I also examined the hairs of *Plaxiphora obtecta,* which are large discrete shafts of cortical material (Fig. 15, Table 1). In sectioned material I found no nerves emerging from the bases of their trichogenous papillae. With this exception, all of the mopaliid hairs that I examined either contained or contacted epidermal neurons (Leise and Cloney, 1982; Leise, 1983). The hairs of *P obtecta* could truly lack innervation, or this lack could be the result of inadequate fixation.

Stalked nodules, such as those in hairs of mopaliid genera, have been observed in the epidermis of many chitons (Fig. 3; Table 2) and repeatedly hypothesized to be tactile (Blumrich, 1891; Plate, 1898, 1902; Knorre, 1925; Thiele, 1929; Haas and Kriesten, 1975; Fischer *et al.,* 1980). However, the papillae that produce these nodules had not been shown to send nerves into the dermis until the work of Leise and Cloney (1982; Leise, 1983). All stalked nodules are not identical, as is discussed below. The functional distinctions between the various types of nodules are unknown.

OCCURRENCE OF SENSORY NODULES IN THE CHITONS

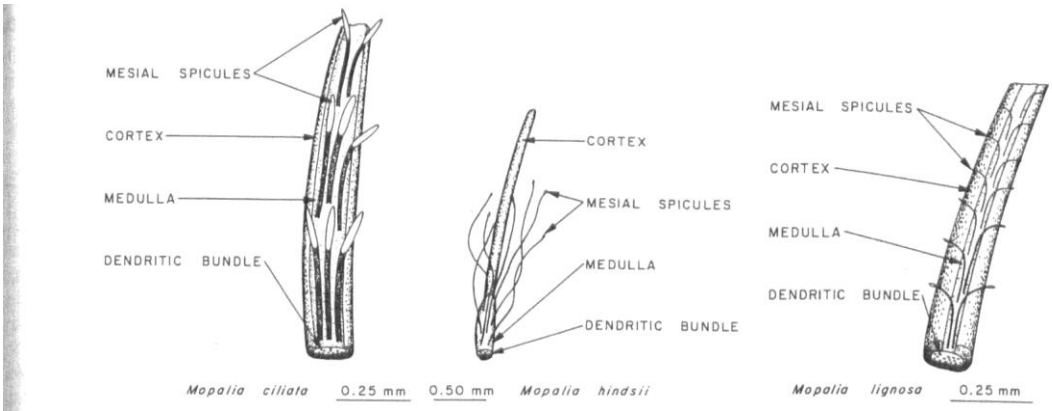
According to Blumrich (1891), all chitons possess a fringe of spicules around the mantle edge. In many cases, the shafts of these marginal spicules contain or surmount a stalked nodule (Table 2) (Plate, 1898, 1902; Knorre, 1925). The hollow shafts of spicules in some species contain more claviform (club-shaped) cellular protrusions that lack a slender stalk (Blumrich, 1891; Plate, 1898, 1902; Knorre, 1925). I examined the ultrastructure of claviform nodules in *Katharina tunicata* and found that they too contain dendrites from epidermal sensory neurons and that the dendrites ramify between vacuolated processes of epidermal supporting cells. Other epidermal protruberances described by Fischer *et al.* (1980) resemble incipient stalked nodules of *Mopalia muscosa* (Leise, 1983). In this review I refer to all of these epidermal protrusions as stalked nodules.

Only on the dorsal surface of the girdle are stalked nodules reported to occur alone (Fig. 3) (Blumrich, 1891; Haas and Kriesten, 1975; Fischer *et al*., 1980; Leise and Cloney, 1982; Leise, 1986). In most cases, dorsal nodules are subjacent to spicules. The ventral girdle in all chitons produces overlapping spicules (Blumrich, 1891; Pilsbry, 1892, 1893; Knorre, 1925; Fischer-Piette and Franc, 1960; Hyman, 1967) and in many cases these spicules also contact sensory nodules (Table 2). Two exceptions are *Placiphorella veleta* and *stimpsoni*, in which the ventral spicules contact stalked cells That are much like those in the dorsal hairs. These cells too will probably prove to be sensory neurons upon further study. Curiously, in *P veleta* the marginal spicules are associated with typical stalked nodules (Plate, 1902; Leise, 1983).

Table 2. Location of sensory nodules in or in conjunction with the designated girdle ornament. Alone indicates in cuticle without attached spicules or hairs [* = animals I examined. Superscripts 1, 2, and 3 designate information from Plate (1898, 1902); Knorre (1925) and Fischer *et al.*, (1980), respectively. NA = not applicable].

Family and Species	Alone	Dorsal Spicules	Marginal Spicules	Ventral Spicules	Dorsal Spicules
Lepidopleuridae					
Lepidopleurus cajetanus[1]		+			
Ischnochitonidae					
Ischnochiton herdmani[2]	–	+	+		NA
*Lepidozona retiporosus**	–	–	+	+	NA
Lepidochitonidae					
*Lepidochitona dentiens**	+	–		+	NA
L. cinerea[2]	+	+			NA
*Tonicella insignis**	–	–			+
Callochitondae					
*Eudoxochiton nobilis**	–	–			–
Chaetopleuridae					
Chaetopleura peruviana[1]	–	–			+
*C. lurida**	–	+	+	+	NA
Mopaliidae					
*Plaxiphora obtecta**	–	–	–	–	–
Katharina tunicata–	–	NA		+	–
*Katharina tunicata**	+	–	+	+	+
*Mopalia ciliata**	+	–			+
*M. lignosa**	+	–	+	+	+
*M. muscosa**	+	–	+	+	+
*Placiphorella velata**	–	–	+	–	–
Chitonidae					
Chiton olivaceus[1]	–	NA	+	+	
Acanthochitonidae					
Acanthochiton fascicularis[3]	–	+	–	+	NA

Of the chitons I studied, in only two species did I find claviform nodules without innervated papillae: *Eudoxochiton nobilis* and *Plaxiphora obtecta*. These animals were fixed in 5% formalin (see Leise, 1983) which does not preserve cellular ulrastructure as well as the combination of glutaraldehyde and osmium tetroxide. Thus, it is possible that the slender 1-2µm in diameter) epidermal nerves were not preserved well enough for me to recognize them. It would be most surprising if these two species alone show no innervated epidermal sensory organs.



13. Diagrams of the external morphology of hairs from three species of *Mopalia*. Note that the cortex does not enclose the medulla in s of *M. hindsii* (from Leise, 1983).

FUNCTIONS OF CHITON HAIRS

The functions of chiton hairs are not well understood although plausible hypotheses abound. Hyman (1967) describes chiton hairs as armature, although chitons bearing hairs are successfully preyed upon by starfish (Mauzey et al., 1968; Paine, 1980), seagulls (Moore, 1975), fish (Ronald Shimek, pers. comm.) and humans. The girdle could be toxic distasteful but it does not provide sufficient protection against predation. Predators tend to eat the foot and viscera, discarding the shell and girdle.

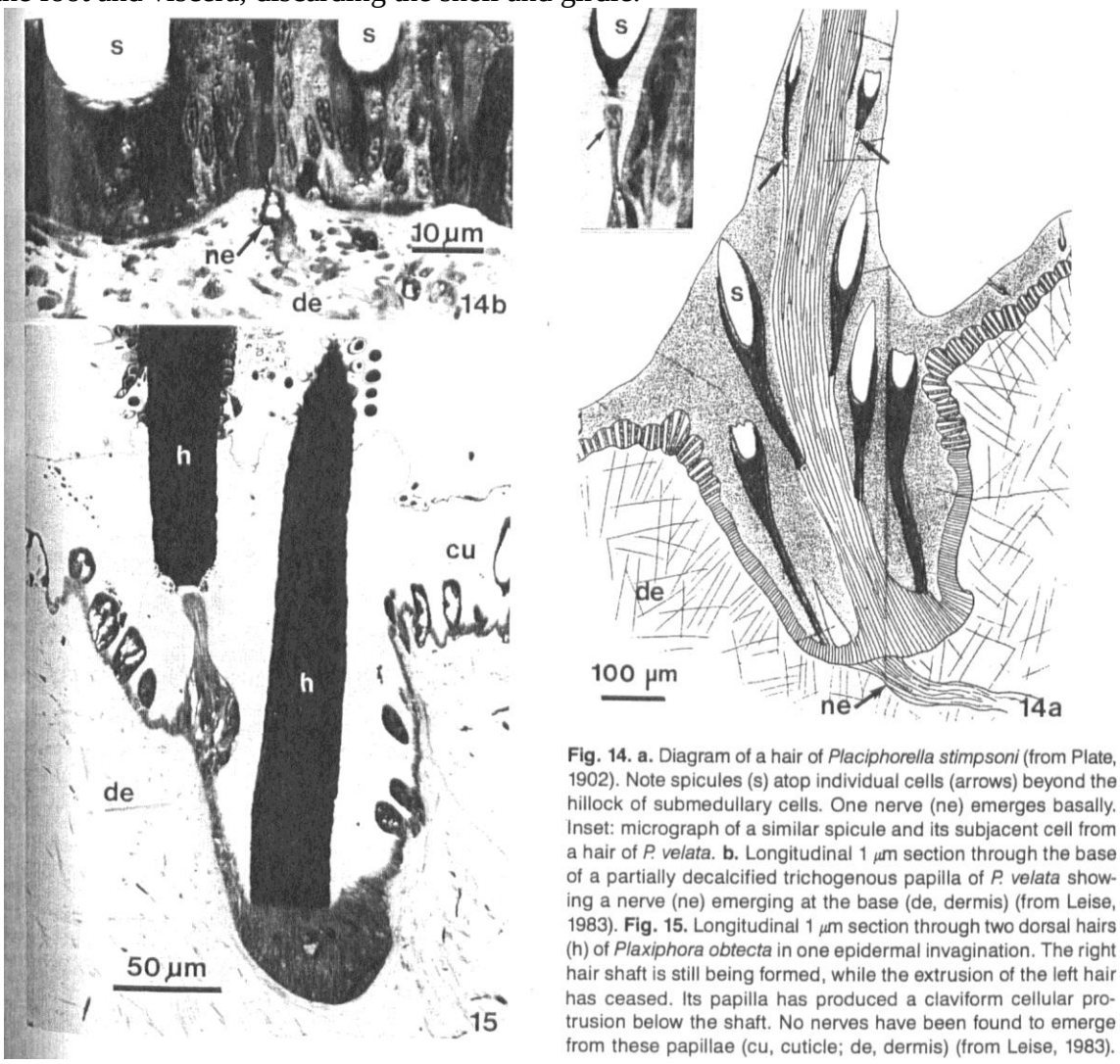


Fig. 14. a. Diagram of a hair of *Placiphorella stimpsoni* (from Plate, 1902). Note spicules (s) atop individual cells (arrows) beyond the hillock of submedullary cells. One nerve (ne) emerges basally. Inset: micrograph of a similar spicule and its subjacent cell from a hair of *P. velata*. **b.** Longitudinal 1 µm section through the base of a partially decalcified trichogenous papilla of *P. velata* showing a nerve (ne) emerging at the base (de, dermis) (from Leise, 1983). **Fig. 15.** Longitudinal 1 µm section through two dorsal hairs (h) of *Plaxiphora obtecta* in one epidermal invagination. The right hair shaft is still being formed, while the extrusion of the left hair has ceased. Its papilla has produced a claviform cellular protrusion below the shaft. No nerves have been found to emerge from these papillae (cu, cuticle; de, dermis) (from Leise, 1983).

Species with large and abundant hairs such as *Mopalia muscosa* often support extensive epiphytic and epifaunal communities (Phillips, 1972). This covering retains water and could protect the animal against desiccation at low tides. This covering could also provide an additional defense against predation. *Pisaster ochraceus* (Brandt, 1835) will feed on *M. muscosa*, but if the chiton is covered with its normal detrital cloak, the starfish may fail to recognize it. After it touches an overgrown chiton, a starfish will ignore it. The basis for this protection, that is, whether the starfish's olfactory or tactile senses are deceived, is unknown. If the starfish contacts the girdle of a clean chiton, it detects a prey item and removes the chiton from the substratum. A chiton cannot escape a hungry starfish nor maintain a sufficiently strong grip on the substratum to avoid being consumed (pers. obs.). A chiton's epiphytic cloak could also afford protection from visual predators. Chitons with well developed epiphytic communities often resemble clumps of algae. Even during high tides, while they are moving and feeding, their identity could be concealed, as their slow rate of motion does not reveal their animal nature.

In addition to providing passive defenses, chiton hairs also mediate active responses from the animal. Chitons whose hairs are bent or pinched will turn away from the source of stimulation, or after several stimuli, tighten their grip on the substratum and remain motionless. This response appears to habituate rapidly, as prolonged or repeated stimulation will soon fail to invoke a response (Leise, 1983).

This tactile aspect of hair function could be most important to juveniles. In *Mopalis muscosa,* hairs first appear at metamorphosis (Leise, 1984) and although they do not initially display all of the adult characteristics, the first sensor/ neurons have differentiated and are presumably operational (Leise, 1986). These young animals take refuge in cracks and crevices in the substratum and their hairs may be important detectors of irregular surface features. Similarly, ventral nodules, which are widespread among the chitons, would give an animal feedback on the surface characteristics of its substratum and allow it to modulate its grip.

Although chiton hairs respond to touch, mechanoreception may not be their primary function. For example, they could be chemoreceptive. However, unlike other molluscan chemoreceptors (Laverack, 1968), the dendrites in the stalled nodules are embedded in the cuticle. I found no pores in the cuticle as exist in insect chemoreceptive hairs (Laverack, 1968). I was also unable to elicit any response from *Mopalis muscosa* upon application to the hairs (without moving the hairs) of various algae or tube feet from a predator starfish *Pisaster ochraceus.*

As previously stated, a sensory function is the most parsimonious explanation for the presence of an innervated integument and cells that resemble sensory neurons. However, this explanation does not exclude the possibility that the basal nerves mediate other functions, such as contraction or secretion. I found no obvious contractile elements in the epidermis of *Mopalis muscosa,* although its skin does secrete the cuticle and ornaments. Epidermal cells in other species such as *Katharina tunicata* extrude pigment granules into the cuticle (Fig. 12) (Leise, 1983). Whether or not the nerves carry axons from neurons mediating epidermal secretion is unknown.

CONCLUSIONS

My results lead me to suggest that most chiton hairs are mechanoreceptors, although hairs are not the only girdle sensory organ. Stalked nodules occur far more widely than hairs, on the marginal and ventral surfaces of what may be a majority of the chitons (Table 2). These nodules are probably important sources of feedback to the animal about the nature of the surface on which it lives. Fischer *et al*. (1980) have also recognized photoreceptors in the girdle of *Acanthochiton fascicularis* that could in part be responsible for this chiton's response to changes in light intensity. Unfortunately, the existence of these girdle sensory organs is not widely recognized.

In her review of the functional morphology of the chiton epidermis, Hyman (1967) did not assimilate Plate's (1902) information about the sensory nature of girdle hairs nor the sentiment from the German literature that stalked nodules are tactile (Blumrich, 1891; Plate, 1898; Knorre, 1925; Thiele, 1929). Since then, the sensory nature of girdle structures has been studied or remarked upon by several authors (Beedham and Trueman, 1967; Haas and Kriesten, 1975; Fischer *et al.,* 1980). Most invertebrate texts include descriptions of chiton sensory organs in the mouth, on the subradular organ, in the buccal cavity, in the pallial grooves, and in the shell plates, but not in the girdle (Hyman, 1967; Meglitch, 1971; Gardiner, 1972; Barnes, 1987; Pearse et al., 1987).

In *Mopalia muscosa,* hairs erode and lose spicules throughout the animals's life. As many species produce hairs and do so constantly during their lifetimes, the benefits from their presence must outweigh their productive costs. Hairs appear to have evolved several times in this class, as large hairs occur in diverse families and can be formed in several ways. Evolutionarily, there appear to be trends towards an increase in the size of girdle ornaments (Pilsbry, 1892; Leise, 1983) and towards an inclusion of sensory organs in these ornaments. Hairs are thus considered to be phytogenetically advanced features, as they also occur in stratigraphically newer families (Smith, 1960) and appear late in an animal's development.

The integument of most molluscs is richly endowed with sensory organs and individual sensory neurons that serve many modalities, including mechanoreception, chemoreception, and photoreception (Laverack, 1968). For the chitons to be "blind" to environmental stimuli over a large portion of their skin would indeed be surprising (Beedham and Trueman, 1967). The work of many authors reviewed here suggests that this is certainly not the case and that the girdle ornaments are not just passive armature but active participants in the lives of these animals.

LITERATURE CITED

Barnes, R. D. 1987. *Invertebrate Zoology* Saunders College, Philadelphia, Pennsylvania. pp. 395-400.

Beedham, G. E. and E. R. Trueman. 1967. The relationship of the mantle and shell of the Polyplacophora in comparison with that of other Mollusca. *Journal of Zoology, London* 151:215a,

Bergenhayn, J. R. M. 1955. Die fossilen schwedischen Loricaten netts einer vorlufigen Revision des Systems der ganzen Klass, Loricata. *Acta Universitets Lundensis* 2, NS 51(8)1-14.

Blumrich, J. 1891. Das integument der Chitonen. *Zeitschrift* lur *Wissenschaftliche Zoologie* 52(3):404-476.

Cloney, R. A. and E. Florey. 1968. The ultrastructure of cephalopod chromatophore organs. *Zeitschrift fiir Zellforschung* 89:250-281

Ferreira, A. J. 1982. The family Lepidochitonidae Iredale, 1914 (Mollusca: Polyplacophora) in the Northeastern Pacific. Vette 25(2):93-138.

Fischer, F. R, W. Maile and M. Renner. 1980. Die Mantelpapillenund Stacheln von *Acanthochiton fascicularis* L. (Motion Polyplacophora). *Zoomorphology* 94:121-131.

Fischer-Piette, E. and A. Franc. 1960. Classe des Polyplacophores, *In: Traitd de Zoologie. Anatomie, Systematique, Biologie* 5121 P.- P. Grasse, ed. pp. 1701-1785. Masson et Cie, Paris.

Gardiner, M. S. 1972. *The Biology of Invertebrates* McGraw-Hill BO Co., New York, New York. pp. 637, 677.

Haas, W. and K. Kriesten. 1975. Studien uber das Perinotum-Epithe und die Bildung der Kalkstacheln von *Lepidochitona cinerel* (L.) (Placophora). *Biomineralisation* 8:92-107.

Hyman, L. H. 1967. *The Invertebrates* VI. *Mollusca* I. McGraw-Hill Bed Co., New York, New York. pp. 74-82.

Knorre, H. von. 1925. Die Schale und die RUckensinnesorganewe *Trachydermon (Chiton) cinereus* L. und die ceylonischechiton[e] der Sammlung Plate. *Jenaische Zeitschrift fiir Naturwasat schaftlichen Medizinische* 61(54):469-632.

Laverack, M. S. 1968. On the receptors of marine invertebrates. *Oceanography and Marine Biology Annual Review* 6:249-324

Leise, E. M. 1983 Chiton integument: Ultrastructure and development of sensory ornaments. Doctoral Dissertation, University of Washington, Seattle, Washington. pp. 1-196.

Leise, E. M. 1984. Chiton integument: Metamorphic changes in *Mopalia muscosa* (Mollusca, Polyplacophora). *Zoomorphology* 104:337-343

Leise, E. M. 1986. Chiton integument: Development of sensory organs in juvenile *Mopalia muscosa. Journal of Morphology 189*

Leise, E. M. and R. A. Cloney. 1982. Chiton integument: Ultrastructure of the sensory hairs of *Mopalia muscosa* (Mollusca: Polyplacophora). *Cell and Tissue Research* 223:43-59.

Loup, E. 1940. Caracteres anatomique de certains Chitons de la cote californienne. *Bruxelles Me'moires du Muscle Royal D'Histoire Naturelle de Belgique* 17:2-41.

Leloup, E. 1942. Contribution a la connaissance des Polyplacophores. I. Famille Mopaliidae, Pilsbry, 1892. *Bruxelles Mdmoires du Muscle Royal D'Histoire Naturelle de Belgique* 25:2-63.

Mauzey, K. P., C. Kirland and P. K. Dayton. 1968. Feeding behavior of asteriods and escape responses of their prey in the Puget Sound region. *Ecology* 49(4):603-619.

Meglitsch, P. A. 1971. *Invertebrate Zoology.* Oxford Press, New York, New York. pp. 291-196.

Moore, M. 1975. Foraging of the western gull *Larus occidentalis* and its impact on the chiton *Nuttallina californica. Veliger* 18 (suppl):51-53.

Paine, R. T. 1980. Food webs: Linkage, interaction strength and community infrastructure. *Journal of Animal Ecology* 49:667-685. Pearse, V., J. Pearse, M. Buchsbaum and R. Buchsbaum. 1987. *Living Invertebrates.* Blackwell Scientific Publications, Palo Alto, California. pp. 319-325.

Phillips, T. 1972. *Mopalia muscosa* Gould (1884) as host to an intertidal community. *Tabulata* 5(1):21-23.

Pilsbry, H. A. 1892. Polyplacophora. *In: Manual of Conchology* Vol. 14 G. W. Tryon, ed. pp. 1-350. Academy of Natural Sciences, Philadelphia, Pennsylvania.

Pilsbry, H. A. 1893. Polyplacophora. *In: Manual of Conchology* Vol. 14 G. W. Tryon, ed. pp. 1-133 Academy of Natural Sciences, Philadelphia, Pennsylvania.

Plate, L. H. 1898. Die Anatomie und Phylogenie der Chitonen. Teil A. *Zoologische Jahrbiicher;* Suppl. 4:1-241.

Plate, L. H. 1902. Die Anatomie und Phylogenie der Chitonen. Teil. B, C. *Zoologische Jahrbiicher,* Suppl. 5:15-216, 281-600.
Reincke, J. 1868. Beitrage zur Bildungsgeschichte der Stacheln im Mantelrande der Chitonen. *Zeitschrift kir Wissenschaftlische Zoologie* 13:305-321.
Smith, A. G. 1960. Amphineura. *In: Treatise on Invertebrate Paleontology.* R. C. Moore, ed. pp. 141-176. University of Kansas Press, Lawrence, Kansas.
Thiele, J. 1929. Erste Klasse des Stammes der Mollusca, Loricata. *In: Handbuch der systematischen Weichtierkunde* 5(1), W. Kiikenthal and T. Krumbach, eds. pp. 1-22. A. Asher and Co., Amsterdam.
Date of manuscript acceptance: 13 November 1987